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[Title page]

Title: Event-related alpha desynchronization in touch – comparing attention and perception

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Highlights

- Endogenous specific alpha ERD observed in a short 500-600ms post cue interval
- Alpha ERD does not differ between attention and perceptual tasks.
- Alpha peaks in frequency later in the endogenous compared to perceptual task.
- Analysis is data driven and does not reduce time or frequency information.

Abstract

An event-related decrease in alpha power contralateral to the presentation of a stimulus is now a well-established phenomenon. Two distinct accounts of the functional role of alpha changes are present in the literature that either focus on alpha changes observed during attentional or simple perceptual tasks. This study directly compares tasks that invoke alpha decreases during exogenous, endogenous and perceptual processing. Using a data driven approach to compare alpha changes we show that alpha decreases differ only between exogenous and endogenous attention tasks for only a short time window, 500-600ms after cue onset. We suggest this indicates a role for alpha in voluntary orientating and stimulus predictability.

Keywords: Attention, Alpha event-related desynchronization, Data-driven, Time-frequency, Somatosensory

Introduction

Event-related changes in alpha power have been observed for a range of different cognitive tasks such as working memory [1], action observation and execution [2] and, relevant to this paper's main concern, attention [e.g. 3,4]. Functional changes in alpha have been observed following shifts of attention to different spatial locations [5]. There are two functionally distinct spatial attentional processes; endogenous and exogenous, both are typically investigated using the Posner cue-target paradigm (see [6] for a review of the cue-target paradigm and associated effects). Typically, changes in alpha power are observed during the cue-target interval (see [7] for a review).

During endogenous spatial attention, modulations of alpha are sensory specific. Covertly orienting visual attention leads to a modulation of alpha power over posterior sites (e.g. [5,8,9]); attention to tactile targets modulates alpha activity over somatosensory regions (e.g. [8, 10, 11, 12, 13]); alpha activity over temporal and parietal regions can be observed following auditory shifts of attention [14]. More specifically, voluntarily orienting attention to a lateralised spatial location results in a decrease in alpha power which is strongest over the hemisphere contralateral to the attended side (in vision and touch) starting approximately 300-400 ms after stimulus onset (e.g. [15]). This event-related desynchronization (ERD), associated with cortical excitability, is thought to reflect increased

information processing and boosts performance for attended stimuli (e.g. [9,16]). The presence of contralateral alpha desynchronization following endogenous attention is well established, however, less is known regarding the effects of alpha during exogenous orienting.

Investigating both endogenous and exogenous attention, Trenner and colleagues [17] presented participants with lateralised tactile cues followed by visual targets. They found contralateral alpha desynchronization approx. 300 ms after cue onset when the participant endogenously oriented attention to the left or right. Moreover, they also observed an ERD around the same time interval even when the cue was non-informative of the upcoming target location. In other words, a similar alpha desynchronization following exogenous orienting, although the effect was smaller. Using visual cues to direct attention to tactile targets, Haegens, Händel and Jensen [18] demonstrate that the predictability of an informative cue directly relates to the degree which alpha power decreases contralateral to an attended location. Specifically, the greatest decrease in contralateral alpha power was observed when the cue was 100% predictive of the location of the target, followed by when the cue was predictive of the target 75% of the time. When the cue was predictive 50% of the time there was minimal amount of alpha power change contralateral to the cued side. These findings suggest that contralateral alpha ERD may be observed following exogenous orienting but is more prominent during endogenous attention. Critically, the exact functional role of contralateral alpha changes is unclear given that exogenous tasks differ from endogenous tasks in both attentional orienting and stimulus predictability.

Alpha ERD is also observed in the absence of both explicit orienting of attention or behavioural response. Simply presenting a stimulus to, for example, a finger leads to alpha desynchronization. Palva, Linkenkaer-Hansen, Näätänen and Palva [19] report alpha power decreases measured over the somatosensory cortex contralateral to the stimuli, when participants merely report on whether a tactile stimulus is perceived or not. Similarly, Gundlach et al. [20] show a contralateral alpha desynchronization following tactile stimulation of one finger, when no response was required by the participant (see also [21,22]). Clearly, simple perceptual processing of a stimulus and exogenous and endogenous attention, result in contralateral alpha ERD. However, it is less known whether alpha ERD across these different tasks are similar in amplitude, time and frequency. The current research addresses this.

We compare three tasks which have shown to modulate contralateral alpha ERD. In all three tasks a tactile stimulus is presented, and time-frequency information is compared in the 1000 ms interval

following the tactile event. In an endogenous attention task, A) participants are presented with a bilateral informative cue directing endogenous attention to the left or right hand. In an exogenous task, B) the cue is lateralised and does not inform the location of an upcoming target. In a third perceptual task, C) a stimulus is presented to only one hand and no responses or explicit shifts of attention are required.

We expect alpha desynchronization to be greatest in the endogenous task reflecting increased cortical excitability as a function of top-down attention to a specific hand and stimulus predictability (e.g. [10, 11, 12, 23]). Comparably, less alpha desynchronization is expected in the exogenous task. This is because the participant is not required to orient endogenous attention and the predictability of any tactile stimuli is low. The inclusion of a perceptual task C) allows us to distinguish whether contralateral alpha changes are more closely linked to endogenous orienting or stimulus predictability, or both, as the perceptual task involves no explicit voluntary orienting of attention but is wholly predictable. If alpha modulations are driven primarily by endogenous orientation, alpha changes should differ between the endogenous condition and both exogenous and perceptual tasks. If predictability drives alpha modulations then differences should be observed between the exogenous task and both the passive and endogenous tasks. However, if alpha modulations are jointly involved in predictability of stimulus and voluntary orienting of attention then alpha modulations should differ only between endogenous and exogenous tasks.

As well as alpha ERD, recent evidence suggests that the specific peak frequency within the alpha band is important and may change as a function of task demands (e.g. [24, 25]). For example, Wutz, Melcher and Samaha [26] demonstrated, while keeping perceptual and cognitive loads constant, task demands modulate peak alpha frequencies and as such conclude that peak alpha frequencies are amenable to top-down control.

The aim of the current study was to compare contralateral alpha desynchronization across three tasks known to result in alpha desynchronization. Previous research has reported alpha changes in response to both perceptual and attentional tasks, but this is the first study to directly compare them. We adopt a novel approach in our analysis by examining amplitude changes without averaging across the time or frequency space. Furthermore, we also consider peak-frequency changes again without compromising time or frequency resolution.

Method

Participants

Twenty-five participants took part in the study. Four participants were excluded due to poor EEG data and three based on behavioural data (see EEG and behavioural analysis sections below). The remaining eighteen participants (15 right handed; 11 females) with a mean age of 26.39 years (range 21-37) were recruited via opportunity sampling. Participants were paid a £20 gift voucher for taking part. All participants gave written informed consent and ethical approval was granted by Middlesex University ethics committee (Ethics No. 1828).

Stimuli and Apparatus

Participants sat in a dimly lit sound-attenuated booth. To mask any noise from the tactile stimulators, white noise at a comfortable listening level was presented throughout the experiment using earphones (Samsung EO-EG920BW). Tactile stimuli were presented using Tactors attached to a TactAmp (Dancer Design Ltd.). Three Tactors were positioned in front of the computer screen, two approximately shoulder width apart and the third centrally placed. A central fixation cross was presented throughout on a PC monitor and a black cloth covered participant's hands. Stimuli were presented using E-Prime v.2 software on a PC which was situated outside of the sound-attenuated booth. Additionally, this PC also sent triggers to a second PC which recorded EEG data using ActiView (BioSemi).

Design and procedure

The study consisted of four different tasks during which EEG was recorded; A – Endogenous, B – Exogenous, C – Perceptual, D – resting state. The order of the tasks was counterbalanced using a Latin square design. All participants initially completed a blinking task to facilitate later ocular correction of EEG data. Participants fixated on a central cross and every 1500 ms the word blink appeared (10 times). EEG data for resting state was recorded but not analysed or reported here.

A - Endogenous Task

Each trial started with a tactile cue presented to both left and right index fingers. The cue was either a single (100 ms) or double tap (30 ms ON – 40 ms OFF – 30 ms ON). For half the participants the single tap indicated attend to the left and the other half attend right (counterbalanced across participants). The participant's task was to orient their attention to one hand based on the cue, whilst fixating their eyes on the fixation cross. Following a 900 ms inter-stimulus interval (ISI) a target (100 ms tap) was presented to either the left or right index finger (see Figure 1). 80% of the time the target appeared to the attended hand and 20% the unattended hand. Participants responded vocally

as quickly as possible to both attended and unattended targets by saying 'Pa' into a voicekey. Once the participant responded there was a variable inter-trial interval (ITI) of 1500<2500 ms before the next trial started. If no response was made, the ITI started after 850 ms. There was a total of 176 trials in the task, split into two blocks of 88 trials each. Overall, there were 128 attended trials (64 left targets and 64 right) and 32 unattended (16 left targets and 16 right). There were 8 catch trials where no target was presented, and the participant was instructed to not respond. There were also 8 fast-filler trials (4 attended and 4 unattended) with an ISI of 400 ms. These trials were not analysed but included to decrease automaticity of responses.

[Insert Fig. 1 here]

B - Exogenous Task

The exogenous task included identical design and procedure to the endogenous task with the following exceptions. On each trial the cue was a lateralised single tap (100 ms) presented to the left or right index finger. There were 176 trials over two blocks. In 80 trials cue and target were presented to the same finger (cued) and in 80 trials opposite fingers (uncued). Participants were instructed to ignore the cue.

C – Perceptual Task

There were 176 trial over two blocks. On each trial a tactile stimulus (100 ms duration) was presented to the participants right index finger. There was a variable interval of 2800<3800 ms presented between each stimulus. Participants were not required to make any response.

Behavioural Analysis

Trials with response times less than 100 ms and greater than 2.5 SD from each participant's overall mean were excluded from analysis. Participants were excluded if they missed more than 20% of targets or responded to more than 50% of catch trials.

EEG recording and data Analysis

EEG (BioSemi Active Two system) was recorded from 128 electrodes at a sample rate of 2048Hz, referenced to the CMS-DRL (common mode sense-driven right leg). Horizontal electro-oculogram (HEOG) was recorded from the outer canthi of the eyes. Offline data were filtered using a zero-phase shift Butterworth band-pass filter (0.13-40Hz), with a 50Hz notch. Data was re-referenced to a common average and blinks were corrected using ICA. Data were then segmented into 3000 ms

epochs, 1500 ms before and 1500 ms after cue onset. Baseline correction was based on 100 ms prior to stimulus onset. Channels F3/4, C3/4, and O1/2, HEOGleft and HEOGright were selected for further analysis. Trials with eye movements (voltage exceeding $\pm 40 \mu\text{V}$ at HEOG electrodes) or with other artefacts (voltage exceeding $\pm 100 \mu\text{V}$ at remaining electrodes) were excluded from further analysis. Based upon non baseline corrected data each segment was analysed using a Complex Morlet wavelet ($c=5$) between 5Hz and 20Hz in 0.1Hz linear step increments. The wavelet analysis was baseline corrected from -600 to -200 ms before stimulus onset on each trial. The data was then averaged separately for each participant and condition and exported for further analysis.

Peak frequency analysis

Typically, individual frequencies are defined by averaging across a temporal window and therefore ignore temporal information (e.g. [20]). We wanted to consider the amplitude, frequency and the time at which a maximal decrease in amplitude took place within a specific region of interest. We chose a region that encapsulated the alpha range 8 – 14Hz and was within a time-period where amplitude modulations have been shown to be maximal, between 200 and 600 ms after stimulus onset. Using customized Matlab scripts, our analysis searched within that frequency and temporal window of interest for the lowest amplitude for each participant. The minimum amplitude and the temporal and frequency location of the maximal amplitude deflection, were used in our ‘peak alpha’ analysis. A one-way repeated measures ANOVA with the factor Task (endogenous, exogenous and perceptual) was conducted, separately for peak frequency, peak time and peak frequency amplitude. All data are based on electrode C3 only.

FDR analysis

To examine differences in amplitude between tasks, across different frequencies during the cue-target interval, we took a data driven approach to the analysis. We conducted multiple t-tests on the amplitude values for each sample in the time frequency matrix; 150 frequency bands by 6144 time samples resulting in 921,600 time frequency points, and for each comparison across the three tasks; Endogenous vs. Exogenous, Endogenous vs. Perceptual and Exogenous vs. Perceptual. Given the high number of comparisons, raw t-statistics produce a conflated chance of finding false positives, however conventional methods used to correct for multiple comparisons would likely result in false negatives. As such, we corrected the resulting p-values from each task comparisons using a False Discovery Rate (FDR) correction. This allowed us to identify regions within the time frequency matrix that differed significantly ($p\text{FDR} < .05$) between tasks. As in our examination of the peak frequencies,

we focused our analysis on electrodes contralateral to the attended right side (electrode C3) so that all tasks were comparable.

Results

Behavioural results

Response times were analysed using a repeated measures ANOVA with the factors Task (exogenous vs. endogenous) and Attention (cued vs. uncued). There were no main effects (all $F_s < 3.13$, all $p_s > 0.09$) but a significant interaction ($F(1, 17) = 32.11$, $p < .001$, $\eta^2 = .17$). Planned paired sample t-tests showed a facilitation effect in the endogenous task ($p = .038$, Cohen's $d = 0.53$) with faster response times for attended ($M = 803.79$ ms, $SD = 181.422$) compared to unattended targets ($M = 822.10$ ms, $SD = 180.08$). In the exogenous task responses to uncued targets ($M = 836.35$ ms, $SD = 176.80$) were faster than cued targets ($M = 863.34$ ms, $SD = 175.01$), demonstrating an inhibition of return ($p < .001$, $d = 1.04$). These results replicate previous effects of tactile attention [27].

EEG results

Amplitude results

The only comparison demonstrating a significant difference within the 8 - 14 Hz frequency range and between 200 ms and 600 ms was between the endogenous and exogenous task (See Figure 3 and Table 1 – 'Figure label B'). Specifically, there was a greater contralateral decrease in amplitude in the endogenous ($M = -0.40$ μV , $SD = .052$) compared to exogenous ($M = -0.11$ μV , $SD = 0.34$) task between 10.1-12.1 Hz in the 486.82-599.61 ms interval. No other differences among the comparisons were observed within the alpha frequency range after the cue onset. Both the comparison between Endogenous vs. Exogenous and Endogenous vs. Perceptual tasks resulted in some low frequency differences immediately after cue onset. Furthermore, Endogenous vs. Perceptual and Exogenous vs. Perceptual resulted in some higher frequency differences. Both the low and high frequency changes are outside of the alpha range and as such are not critical to our concerns but all regions that show a significant difference between tasks are described in full in Table 1.

[Insert Fig. 2 & 3; Table 1 here]

Peak alpha results

There were no main effects of Task on peak frequency ($F(2, 34) = 1.27$, $p = .29$, $\eta^2 = .07$, $BF_{10} = 0.43$) (see Figure 4, top) or peak amplitude ($F(2, 34) = 0.88$, $p = .42$, $\eta^2 = .05$, $BF_{10} = 0.28$) (see Figure 4, bottom). There was a main effect of Task on peak time ($F(2,34) = 3.47$, $p = .04$, $\eta^2 = .17$) and a

Bonferroni corrected follow-up analysis indicated that the alpha peak was significantly later in the endogenous ($M = 470.04$ ms, $SD = 71.83$) compared to the Perceptual task ($M = 384.36$ ms, $SD = 110.12$) ($t(17) = 2.75$, $p = 0.03$, *Cohen's d* = 0.65) (see Figure 4, middle). There was no difference between Endogenous and Exogenous ($t(17) = 2.16$, $p = 0.09$, $BF_{10} = 1.56$) or Exogenous and Perceptual tasks ($t(17) = 2.16$, $p = 1.00$, $BF_{10} = 0.24$).

[Insert Fig. 4 here]

Discussion

The present study aimed to contrast changes within the alpha frequency contralateral to the stimulus in three separate tasks; endogenous, exogenous and perceptual. We examined both peak frequency changes and amplitude comparisons across the tasks. Amplitude differences were explored by comparing each time-frequency unit, for each comparison, and correcting for multiple comparisons. This resulted in a clear difference within the alpha frequency bandwidth (10 – 12 Hz) approximately 500-600 ms after cue onset between the endogenous and exogenous task. Specifically, there was a greater ERD in alpha amplitude in the endogenous compared to the exogenous task. This suggests that alpha amplitude decreases may play a specific role in the voluntary orienting of attention and are less likely related to stimulus driven attentional demands. Furthermore, no differences in alpha modulations were found between endogenous or exogenous and perceptual tasks.

The now well established [8, 10, 11, 12, 13] decrease in alpha amplitude contralateral to the attended side for the voluntary orientation of spatial attention compared to exogenous orientation is replicated in our study. Our relatively late and short-lived difference (Figure label B) seemingly reflects voluntary shifts of attention – a processes unique to the endogenous task. However, similar previous research has reported alpha decreases over a longer time window [8, 13, 23]. Our data suggest that only a specific time-frequency window component of the contralateral alpha modulation is related to endogenous orientation. The prolonged alpha typically observed is potentially also driven by alpha activity as a function of temporal attention in the cue-target interval [13]. Indeed, a more widespread alpha desynchronization effect is also observed in the time-frequency plots for each task in the current study (see Figure 2). The timing of the target was identical in the exogenous and endogenous tasks, resulting in any oscillatory effects of temporal expectation cancelling each other out when contrasting the tasks (Figure 3). In other words, the 500-

600 ms interval observed in the current study is likely specific to orienting of endogenous spatial attention.

Interestingly, changes in the alpha frequency bandwidth did not differ between either explicit attentional task (endogenous and exogenous) and the perceptual task. Previous research has reported alpha decreases contralateral to stimulus presentation during attentional tasks [8, 10, 11, 12, 13] and perceptual ones [19, 20, 21, 22], but this is the first study to directly compare them. We suggest our data demonstrate a functional role for event related changes in alpha that are linked to both voluntary orientation of attention and predictability of stimuli. Specifically, we argue, no differences between the perceptual task and the endogenous task are the result of similar predictability of stimulus. No differences between the perceptual task and the exogenous task are the result of a similar lack of voluntary attention. Of course, this somewhat speculative position needs further investigation as it is based on a combination of both positive and null results. However, this is the first study to make such data-driven comparisons and we feel will better help disentangle perceptual and attentional roles of alpha changes.

Although we focus on contralateral alpha changes as they relate to perceptual and attentional processes, there are several other notable differences within other frequency bandwidths found among our data. First, we see low frequency amplitude increases in the exogenous and perceptual task compared to the endogenous task (Figure label A and D). This likely reflects the fact that only the endogenous task used bilateral stimuli, and this is most probably a frequency description of an ERP to unilateral stimuli, absent in the endogenous condition, as found in previous research [28]. Furthermore, higher frequency changes (< 13.5 Hz) appear later in the epoch (< 700 ms) and show greater amplitude decreases in the attentional tasks (both endogenous and exogenous) compared to the perceptual tasks (Figure 3, labels G-J). These likely reflect beta decreases in amplitude common to both voluntary and stimulus driven attentional orientating as has been suggested by others [13]. The other small differences observed in amplitude comparisons (Figure 3, labels C, E & F) span less than 1 Hz and less than 65 ms. Given that FDR corrections are made at the population level they include a likely 5% of false positives [29], we suggest that these small differences are unlikely to be indicative of underlying cognitive differences.

We also explored differences in the peak frequency changes for the separate attentional tasks. Unlike in previous research we include temporal information in our estimation of peak frequencies. In doing so we show that during the endogenous task peak frequency changes occur later than during the perception task. Whilst previous research has shown that differences in peak frequencies are indicative of cognitive load (e.g. [24]) to our knowledge none have examined *when* the alpha

frequency peaks. Given that a later peak in alpha is found in endogenous compared to perceptual this may be indicative of coalitional attentional processes requiring greater effort and conscious control compared to passive perception. Arguably, time differences in alpha peak frequency may simply be a function of amplitude changes as a function of time. In other words, it may be true that there is an earlier decrease in amplitude for one condition compared to the other rather than a difference in peak frequency per se. However, given that no differences between the endogenous task and perceptual task were observed in the amplitude comparisons this seems an unlikely explanation.

Overall, we suggest that the contralateral alpha amplitude decrease found during endogenous attention, only a short window (approximately between 500-600 ms), is uniquely associated with voluntary attentional shifting. Furthermore, that alpha amplitude changes are indicative of both endogenous orientation and predictability of the stimulus. Tentatively we suggest that when alpha peaks may also provide some information about underlying attentional processes and should be explored further.

Conflict of interest: None declared

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ACCEPTED MANUSCRIPT

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Figure legend

Figure 1. Schematic view of events in a trial for each of the Endogenous task (A), Exogenous task (B) and Perceptual task (C). Note: Inter-stimulus interval (ISI), Inter-trial interval (ITI).

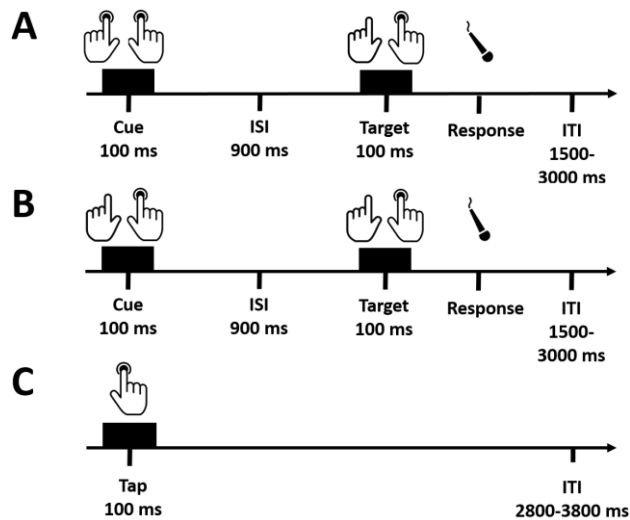


Figure 2. Grand averaged frequency spectra for each task at C3 electrode. The colour represents amplitude (μV) as a function of time (x-axis) and frequency (y-axis) in each task. In tasks A and B, the participant were presented with a cue (time 0 ms, black arrow) followed by a target (white arrow). In the perceptual task (C) the stimulus (grey arrow) required no response. In all three tasks, data was baseline corrected to -600 to -200 ms before cue/stimulus onset (BC, white solid line) and analysis was based on the 200-600 ms time interval post stimulus onset, in the 8-14 Hz frequency range.

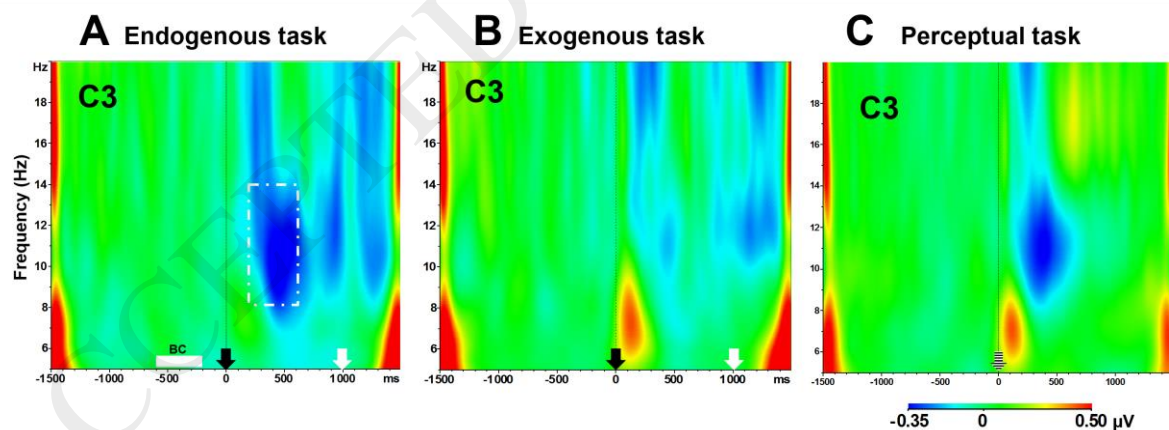


Figure 3. False Discovery Rate (FDR) corrected contrasts between the tasks. Yellow areas represent significant differences between tasks and blue non-significant. Letters correspond to labels presented in Table 1. Y-axis is frequency (in Hertz) and x-axis time (in milliseconds).

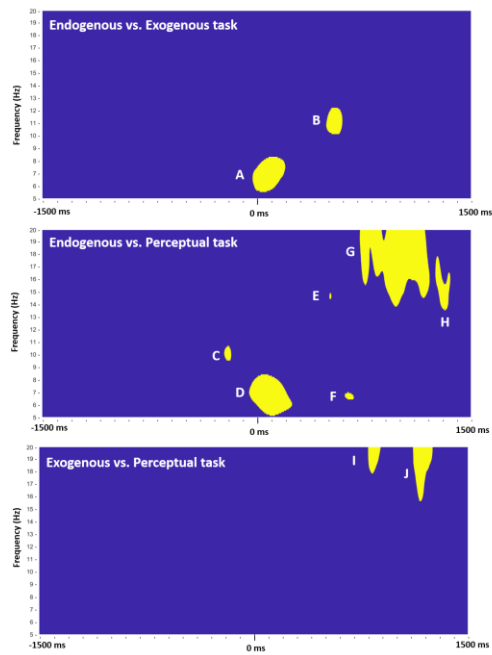


Figure 4. *Top.* Bars represent average peak frequency across the three tasks. *Middle.* The timing of the peak desynchronization relative to stimulus onset in each task. There was a significant difference in peak time onset between the endogenous and perceptual tasks ($*p<.05$). *Bottom.* The amplitude (in microvolts) of the extracted peak in the three tasks. Error bars represent standard error (SE).

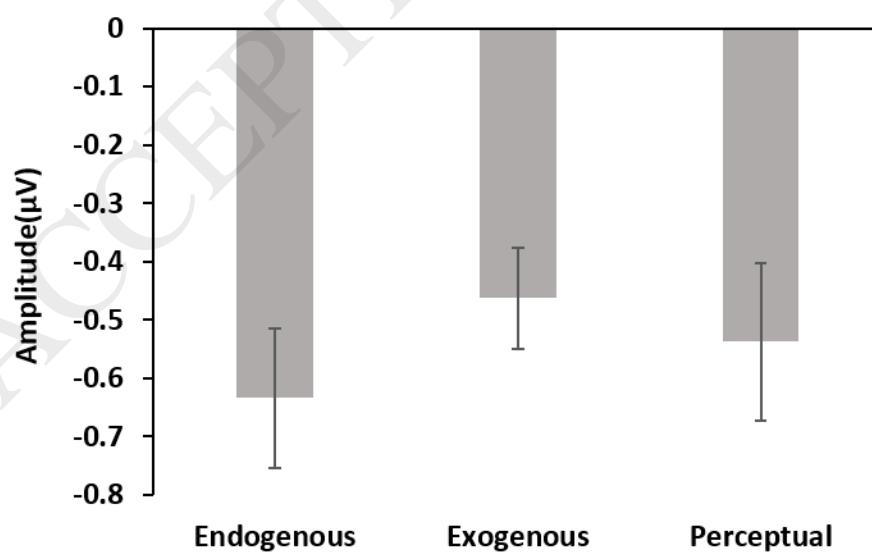
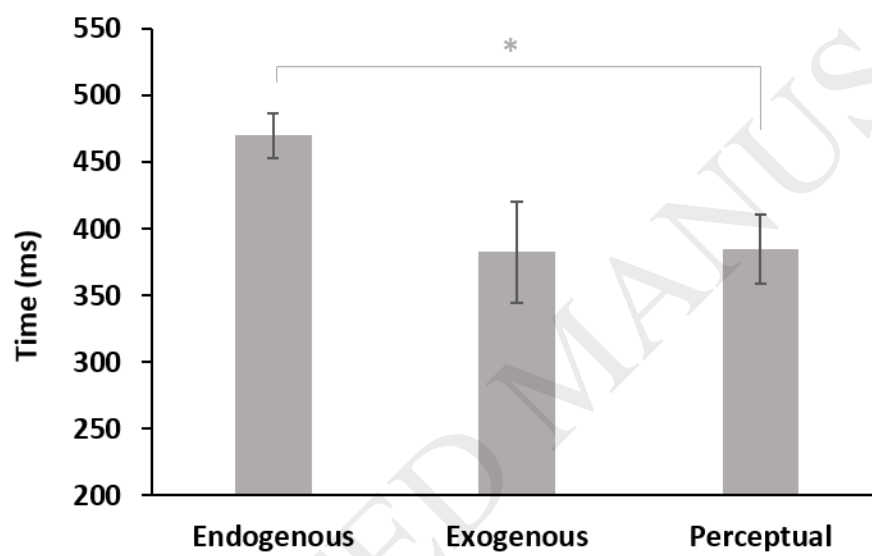
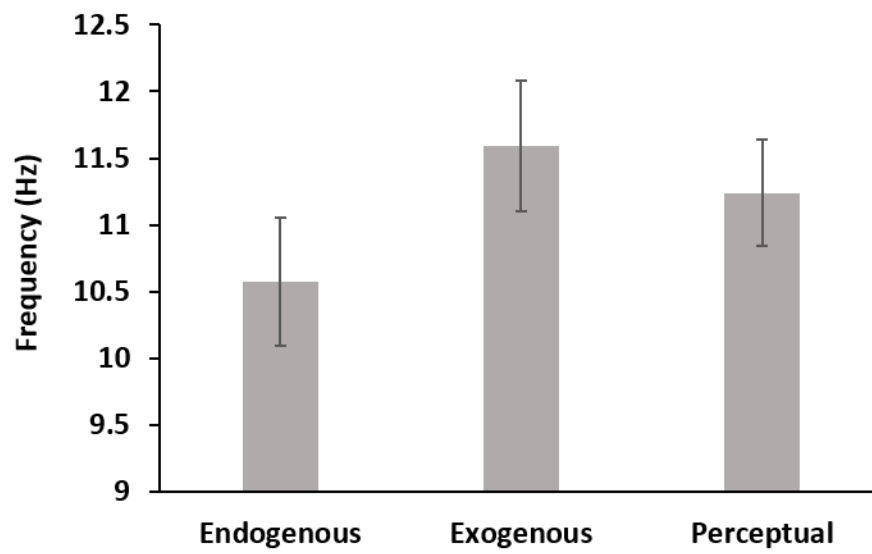


Table 1. The table shows the values related to the time-frequency areas that differed significantly following FDR corrected comparisons in Figure 3, for each

	Figure label	Min Freq (Hz)	Max Freq (Hz)	Onset (ms)	Offset (ms)	Endo M (μ V)	Endo (SD)	Exo M (μ V)	Exo (SD)	Perceptual M (μ V)	Perceptual (SD)	of the
Endogenous Vs. Exogenous	A	5.5	8.2	-28.81	199.70	0.0418	0.3681	0.3647	0.4391	-	-	
	B	10.1	12.1	486.82	599.61	-0.3977	0.5156	-0.1085	0.3435	-	-	
Endogenous Vs. Perceptual	C	9.5	10.6	-226.56	-178.22	-0.0499	0.2211	-	-	0.0893	0.202	
	D	5.1	8.3	-52.73	677.73	0.0318	0.3449	-	-	0.3358	0.31	
	E	14.4	14.8	509.76	523.44	-0.1412	0.2242	-	-	0.0371	0.212	
	F	6.5	6.9	617.19	680.66	-0.1558	0.1943	-	-	0.0611	0.161	
	G	13.8	19.9	722.66	1210.94	-0.1707	0.2237	-	-	0.1425	0.2415	
	H	13.5	17.7	1251.46	1355.47	-0.1963	0.2508	-	-	0.0802	0.1896	
Exogenous Vs. Perceptual	I	17.8	19.9	801.76	889.65	-	-	-0.179	0.1964	0.1813	0.2059	
	J	15.6	19.9	1116.21	1252.93	-	-	-0.2422	0.2037	0.126	0.22	

Figure labels (A-J).

Note. Min/Max Freq.– Lowest and highest frequency (in hertz) of the significant (yellow) area of the figure label. Onset/Offset – the onset and offset of the significant area in time (milliseconds). Endogenous task (Endo); Exogenous task (Exo); Perceptual task (Perceptual); M – Mean amplitude of the ERD/ERS.

